RELATIVE GAINS AND LOSSES IN RISKY CHOICE

by

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Abstract

The present experiments examined the effect of different uncertain-reward magnitudes (i.e., gains and losses) on global and local probabilistic choice behavior in rats. In two experiments, rats were given a choice between a variable-amount certain outcome that delivered 2 or 4 pellets and a variable-amount uncertain outcome that probabilistically delivered a larger reward. In Experiment 1, the larger uncertain outcome was always 11 pellets and different groups received 1, 2, or 4 pellets for the uncertain small reward. In Experiment 2, the uncertain small reward was always 4 pellets and different groups received 6, 9, or 11 pellets for the uncertain large reward. In both experiments, the rats increased their uncertain choice behavior with the probability of uncertain food. In Experiment 1, the magnitude of the uncertain small outcome affected choice behavior; there was no such effect of the uncertain large reward magnitude in Experiment 2. The group differences in choice behavior suggest that the expected value of the certain choice served as a reference point distinguishing uncertain gains and losses, and that the rats exhibited differential sensitivities to such outcomes. As some extant theoretical frameworks of choice behavior seem unable to account for all of the present data, a possible mechanism for the present results is proposed. These results emphasize the importance of identifying the choice outcomes that constitute gains and losses in animals such that the effects of prior uncertain gains and losses on subsequent choice behavior can be adequately and comprehensively understood.

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Chapter 1 - Introduction

The analysis of risk-sensitive decision making has become a well-established area of research within fields such as human judgment and decision making, animal choice behavior, and neuroeconomics (e.g., Platt & Huettel, 2008; Weber, Shafir, & Blais, 2004). Risky choice tasks typically involve giving individuals the choice between two options: a guaranteed (certain) small-magnitude outcome and a probabilistic (uncertain) large-magnitude outcome (e.g., Rachlin, Raineri, & Cross, 1991). By varying the probability of receiving the larger outcome, it is possible to determine the rate at which an individual's subjective value of the larger reward decreases as the probability of receiving it decreases (i.e., probability discounting; Rachlin et al., 1991). Additionally, manipulation of the magnitude of the certain small or uncertain large outcome provides an index of reward magnitude sensitivity within the same probabilistic choice task (Dai, Grace, & Kemp, 2009; Green, Myerson, & Ostaszewski, 1999; Myerson, Green, Hanson, Holt, & Estle, 2003). Accordingly, both the magnitude and probability of the choice outcomes affect probabilistic choice behavior in humans (e.g., Myerson et al., 2003). Interestingly, previous research has shown differential discounting of probabilistic rewards in gamblers (Holt, Green, & Myerson, 2003), cigarette smokers (Reynolds, Richards, Horn, & Karraker, 2004), and individuals with a high percent body fat (Rasmussen, Lawyer, & Reilly, 2010), as well as a trend toward differential effects of reward magnitude on probability discounting in gamblers versus non-gamblers (see Holt et al., 2003). Therefore, in conjunction with the prevalence of risky behaviors such as pathological gambling (Shaffer, Hall, & Vander Bilt, 1999; Shaffer & Korn, 2002) and drug use and abuse (Compton, Thomas, Stinson, & Grant, 2007) and the recent interests in developing an adequate animal model of gambling behavior

(Madden, Ewan, & Lagorio, 2007; Potenza, 2009; Weatherly & Derenne, 2007; Winstanley, 2011), such results reflect the necessity to determine the psychological and neurobiological mechanisms of risky (or probabilistic) decision making.

While several well established results have emerged from the human and animal probabilistic choice literatures (as described above), one aspect of probabilistic choice behavior that has received relatively less attention is the effect of the outcomes of previous choices on subsequent choice behavior. As previous research has shown differences in probabilistic choice behavior depending on whether such choices are offered in isolation or in sequence (Keren & Wagenaar, 1987), molecular analyses of choice behavior can provide critical insight into the trial-by-trial (local) mechanisms of probabilistic choice that have not been elucidated within non-sequential choice paradigms. The importance of such analyses has indeed been recognized (see Dixon, Hayes, Rehfeldt, & Ebbs, 1998; Kalenscher & van Wingerden, 2011). Accordingly, several species, including rats, bees, monkeys, and humans, have been shown to not only be affected by the experimenter-controlled manipulations of choice tasks, but also by the outcomes of previous choices (e.g., Demaree, Burns, DeDonno, Agarwala, & Everhart, 2012; Dixon et al., 1998; Dukas & Real, 1993; Evenden & Robbins, 1984; Fülöp & Menzel, 2000; Greggers & Menzel, 1993; Hayden & Platt, 2009; Heilbronner & Hayden, 2013; Leopard, 1978; Marshall & Kirkpatrick, 2013; McCoy & Platt, 2005; Montague, Dayan, Person, & Sejnowski, 1995; St. Onge, Stopper, Zahm, & Floresco, 2012; Stopper & Floresco, 2011). For example, McCoy and Platt (2005) gave macaques a choice between an outcome that delivered a constant amount of reward and an outcome that delivered a variable amount of reward with an expected value equivalent to the constant outcome; these monkeys were more likely to make riskier choices for the variable reward outcome as the magnitude of the previous outcome deviated more from the expected value of the outcomes (for a similar result in humans, see Hayden & Platt, 2009). Therefore, despite the independence of consecutive trials, probabilistic choice behavior appears to be partially dependent on previous outcomes (but see, e.g., Caraco, Martindale, & Whittam, 1980).

A special case of local influences on choice behavior is a general tendency to repeat the same behavior following a "win" (or gain; i.e., win-stay), and a reduced propensity to repeat the same behavior following a "loss" (i.e., lose-shift; Ayton & Fischer, 2004; Evenden & Robbins, 1984; Marshall & Kirkpatrick, 2013; Gilovich, Vallone, & Tversky, 1985; Hayden & Platt, 2009; St. Onge et al., 2012; Stopper & Floresco, 2011; Stopper, Green, & Floresco, 2012; Thorndike, 1911; but see Gehring & Willoughby, 2002; Goyer, Woldorff, & Huettel, 2008; Riba, Krämer, Heldmann, Richter, & Münte, 2008). For example, Floresco and colleagues have repeatedly shown that rats tended to stay with the probabilistic (risky) choice following a probabilistic four-pellet gain; however, following a probabilistic zero-pellet loss, the same rats were relatively more likely to make a choice for a certain one-pellet outcome (St. Onge et al., 2012; Stopper & Floresco, 2011; Stopper et al., 2012). Such choice behavior is indicative of win-stay / lose-shift behavior. Similarly, Marshall and Kirkpatrick (2013) gave rats a choice between a certain outcome that always delivered food (either one or three pellets) and an uncertain outcome that probabilistically delivered food (zero, three, or nine pellets). These authors showed that rats were significantly more likely to make an uncertain choice after having just received food for a previous uncertain choice (gain) than after having not received food for a previous uncertain choice (loss), indicative of win-stay / lose-shift behavior. Interestingly, as many risky-choice paradigms, as well as casino games (see Crossman, 1983), do not adjust the probability of winning (or losing) as a function of the most recent outcome, a rational decision maker should not be differentially affected by whether or not the previous outcome was a win or a loss (see Gehring & Willoughby, 2002). Nevertheless, in conjunction with the studies described above, the strong effect of the previous outcome(s) suggests that human and non-human animal decision makers are considerably influenced by both global and local factors within risky choice tasks (e.g., riskiness of reward, and previous outcomes, respectively), and that the corresponding psychological processes warrant further investigation.

Given such effects of previous outcomes on subsequent choice behavior, it is important to determine what distinguishes gains from losses. Theoretically, gains and losses are regarded as such relative to some subjective reference point (Kahneman & Tversky, 1979; Hastie & Dawes, 2010; Tversky & Kahneman, 1981; Wang & Johnson, 2012). For instance, reference points have been suggested to reflect an individual's current state (i.e., what an individual currently has), and positive and negative deviations from this state reflect gains and losses, respectively (Kahneman & Tversky, 1979). This conceptualization of a reference point is reasonable in regards to the human probabilistic choice literature, as an individual's monetary status can be easily decreased or increased. However, given the use of consumable rewards within the animal choice literature, the treatment of gains and losses relative to a current state is unlikely, as the consumption of food cannot be readily undone when a loss is experienced. Accordingly, gains and losses have been alternatively suggested to refer to positive reward outcomes that are greater than or less than, respectively, the expected value of a choice (e.g., receiving one food pellet when four food pellets were expected). Current theoretical frameworks of probabilistic choice behavior have indeed considered that the expected value of a choice (or expected state) may serve as a reference point for corresponding gains and losses (e.g., Kahneman & Tversky, 1979; Sutton & Barto, 1998).

Interestingly, while previous empirical research has shown differential choice behavior following outcomes greater than or less than the expected value of a choice (e.g., Stopper & Floresco, 2011), such research may have complicated the ability to determine whether the expected value of a choice serves as the true reference point for corresponding gains and losses. For example, if given the choice between a certain outcome that always delivers one pellet and an uncertain outcome that probabilistically delivers zero or four pellets (see Stopper & Floresco, 2011), the uncertain four-pellet outcome may be considered a gain given several possible reference points. First, the four-pellet outcome may be regarded as a gain because it is greater than the expected value of the uncertain choice, suggesting that the corresponding expected value is the reference point (as the animal cannot be informed of the expected value of a choice, the value of a choice must be learned; however, as the animal is likely to experience the expected value after multiple choices, subsequent references to the expected value of a choice will refer to this learned value). Second, the four-pellet outcome may be regarded as a gain because it is a positively-valued food reward. Here, the four-pellet outcome may be regarded as a gain because it compensates for the energy expended while responding for the choice. Accordingly, the omission of food reward would be considered a loss, ultimately suggesting that the corresponding reference point would be approximately zero. Lastly, an alternative explanation for why the four-pellet outcome may be treated as a gain is because its magnitude is greater than the expected value of the alternative *certain* choice. Thus, uncertain gains and losses may be regarded as such in consideration of what could have been received had a different choice been made. Therefore, a four-pellet food reward may be regarded as an uncertain gain given several different reference points. However, as previous studies have either equated the expected values of different choices (e.g., Hayden & Platt, 2009; McCoy & Platt, 2005) or collapsed across different expected values of the probabilistic choice for data analysis (e.g., St. Onge et al., 2012; Stopper & Floresco, 2011; Stopper et al., 2012), these possibilities, to our knowledge, have yet to be thoroughly elucidated.

Accordingly, the goal of the present experiment was to determine the reference point that distinguishes gains from losses in rats by analyzing the effects of previous outcomes on subsequent choice behavior. The current paradigm was similar to that used by Marshall and Kirkpatrick (2013), in which both certain choices and rewarded uncertain choices involved variable-reward outcomes. Such outcomes, in conjunction with the probabilistic food omissions following uncertain choices, permit evaluation of the different reference-point explanations described above. Specifically, if a value of zero serves to distinguish probabilistic gains and losses (i.e., a zero-based reference point), then the rats should respond relatively similarly following all positive probabilistic food rewards, but differently relative to the choice behavior that follows probabilistic food omission. Alternatively, if probabilistic gains and losses are differentiated depending on their relationship to the expected value of the uncertain choice (i.e., an uncertain-choice-based reference point), then the rats would be expected to show differences in choice behavior following outcomes greater than and less than the uncertain choice's expected value. However, if uncertain gains and losses are treated in terms of how their magnitudes compare to the value of the certain choice (i.e., a certain-choice-based reference point), then the rats should respond differently following uncertain food rewards greater than and less than the value of the certain choice, but similarly following uncertain food rewards with magnitudes greater than the value of the certain choice.

Chapter 2 - Experiment 1

Method

Animals

Twenty-four experimentally-naive male Sprague-Dawley rats (Charles River, Portage, MI) were used in the experiment. They arrived at the facility (Kansas State University, Manhattan, KS) at approximately 45 days of age. The rats were pair-housed in a dimly lit (red light) colony room that was set to a reverse 12-hr light:dark schedule (lights off at approximately 6 am). The rats were tested during the dark phase. There was ad libitum access to water in the home cages and in the experimental chambers. The rats were maintained at approximately 85% of their projected ad libitum weight during the experiment, based on growth-curve charts obtained from the supplier. When supplementary feeding was required following an experimental session, the rats were fed in their home cages (together or individually) approximately 1 hr after being returned to the colony room (see Bacotti, 1976; Smethells, Fox, Andrews, & Reilly, 2012).

Apparatus

The experiment was conducted in 24 operant chambers (Med-Associates, St. Albans, VT) each housed within sound-attenuating, ventilated boxes (74 × 38 × 60 cm). Each operant chamber (25 × 30 × 30 cm) was equipped with a stainless steel grid floor; two stainless steel walls (front and back); and a transparent polycarbonate side wall, ceiling, and door. Two pellet dispensers (ENV-203), mounted on the outside of the operant chamber, delivered 45-mg food pellets (Bio-Serv, Frenchtown, NJ) to a food cup (ENV-200R7) that was centered on the lower section of the front wall. Head entries into the food magazine were transduced by an infrared photobeam (ENV-254). Two retractable levers (ENV-112CM) were located on opposite sides of the food cup. Water was always available from a sipper tube that protruded through the back wall of the chamber. Experimental events were controlled and recorded with 2-ms resolution by the software program MED-PC IV (Tatham & Zurn, 1989).

Procedure

Pre-training

The rats were first trained to eat from the food magazine. Magazine training lasted for one session. Food pellets were delivered to the food magazine on a random-time 60-s schedule of reinforcement. The rats earned approximately 120 reinforcers in the 2 hr session. The rats were then trained to press both the left and right levers. Each of the two lever-press training sessions began with a fixed ratio (FR) 1 schedule of reinforcement and lasted until 20 reinforcers were delivered on each lever. The FR 1 was followed by a random ratio (RR) 3 schedule of reinforcement, which lasted until 20 reinforcers were delivered for lever pressing on both sides. The RR 3 was then followed by an RR 5, which lasted until the rats earned 20 reinforcers on each lever.

Training

Each session consisted of 8 forced choice trials followed by a series of free choice trials. On forced choice trials, one lever was inserted into the chamber. Each lever corresponded to one of two choices – a choice with a certain outcome and a choice with an uncertain outcome; lever assignment was counterbalanced within each pair of rats. When the lever was pressed, a fixed interval (FI) 20-s schedule began; the first lever press after 20 s resulted in retraction of the lever and food delivery. If the presented lever corresponded to the certain outcome, then either 2 or 4 pellets were delivered; the probability of delivery of each magnitude was .50. If the presented forced choice lever corresponded to the uncertain outcome, then either a smaller or larger amount of food was delivered; the probability of delivery of each magnitude was .50. The larger amount was 11 pellets in all three groups, but the smaller amount differed across groups (see Table 2.1). The groups (*n* = 8) were formed by random assignment of pairs of rats. The smaller amount was 1, 2, and 4 pellets for Groups 1-11, 2-11, and 4-11, respectively. In the eight forced choice trials, food was delivered following all forced choices of the uncertain outcome. Each of the food amounts for the certain choice and uncertain choice were presented twice each in the 8 forced choice trials in a random order. A 10-s inter-trial interval (ITI) followed food delivery before the onset of the next trial.

On free choice trials, two levers were inserted into the chamber. A choice was made by pressing one of the levers, causing the other lever to retract. The first lever press after 20 s resulted in outcome delivery and initiation of the 10-s ITI. Certain choices terminated with the equally probable delivery of 2 or 4 food pellets, and uncertain choices probabilistically terminated in food delivery, with the small and large rewards delivered with equal probability. In different phases, the probability of food delivery following an uncertain choice was .1, .25, .33, .50, .67, .75, or .90.

The probability of uncertain food delivery varied across phases (Table 2.1). All rats were first exposed to a condition in which uncertain food was delivered with a probability of .50. Phase 2 involved a reversal of the lever assignments (i.e., if the certain choice was assigned to the left lever for one rat in Phase 1, it was reassigned to the right lever in Phase 2). For Phases 3-8, the rats in each group were partitioned into two subgroups that experienced the probabilities of uncertain food delivery in different orders (Table 2.1): .75, .33, .67, .25, .90, and .10 (Order 1), or 25, .67, .33, .75, .10, and .90 (Order 2). The assignment to each order was based on uncertain choice behavior in Phase 2, with the four most risk-averse rats from each group being assigned to Order 1. In Phase 9, all of the rats were returned to the probability of .50.

Phases 1 and 2 lasted for 20 sessions each. Phase 3 lasted for 22 sessions. After the first 12 sessions of Phase 3, the maximum number of free choice trials was reduced from 160 to 100 to better maintain the rats' weights at approximately 85% of their ad libitum weights (see *Animals*) and this change was maintained for the rest of the experiment. Phase 4 lasted for 11 sessions. Phases 5-9 lasted for 10 sessions each. Each session terminated after all free choice trials were completed or after approximately 2 hr, whichever occurred first.

Data analysis

The final five sessions of Phases 3-9 were used for data analyses, with the exception of one rat that did not complete Phase 9, in which the first 100 choice trials of each session in Phase 2 were used instead. Statistical analyses were collapsed across the different orders of exposure to the probabilities of uncertain food delivery. Unless described otherwise, Tukey's Honestly Significant Difference test was employed for post hoc analyses of significant effects and interactions.

Results and Discussion

Molar analysis

Figure 2.1 (top panel) shows the log odds of uncertain choices as a function of the probability of uncertain food delivery. The log odds of choice behavior offered a more sensitive measure to detect differences in choice behavior, and removed the constraining limits of 0 and 1 imposed by measures of choice behavior in terms of proportions or percentages. An empirical log odds formulation was employed to correct for exclusive choices: log odds = $\ln([N_U + 0.5]/[N_C + 0.5])$, where N_U was the number of uncertain choices and N_C was the number of certain choices, such that the log odds was the natural logarithm of the odds ratio of the number of uncertain to certain choices (see Garcia & Kirkpatrick, 2013, for a similar approach). A value of 0.5 was added to the numerator and the denominator such that the log odds for exclusive-choice behavior could be computed (see Haldane, 1956); for example, without such a modification, the absence of a certain choice would produce a denominator of zero and an odds ratio of positive infinity. The horizontal line in Figure 2.1 (top panel) reflects neutrality where there were an equivalent number of uncertain choices and certain choices. Values below this line reflect risk aversion (more certain than uncertain choices), and values above it reflect risk proneness (more uncertain than certain choices). Figure 2.1 (top panel) shows that all groups exhibited a general increase in uncertain choices as the probability of uncertain food increased. Furthermore, Group 4-11 made more uncertain choices, followed by Group 2-11 and then Group 1-11.

An analysis of variance (ANOVA) with probability as the within groups factor and uncertain-small (U-S) reward magnitude as the between groups factor (1-11, 2-11, and 4-11) revealed main effects of probability, $F(6, 126) = 10.73$, $p < .001$, and group, $F(2, 21) = 7.64$, $p = .003$, but no Probability × Group interaction, $F(12, 126) = 1.27$, $p = .245$. Post hoc Tukey comparisons revealed that Group 1-11 chose the uncertain outcome significantly less than Group 4-11, $p < .05$, but that Groups 1-11 and 2-11 as well as Groups 2-11 and 4-11 did not significantly differ, *p*s > .05. Therefore, in conjunction with previous probabilistic choice research (Cardinal & Howes, 2005; Marshall & Kirkpatrick, 2013; Mazur, 1988; Mobini et al., 2002; St. Onge et al., 2012; Stopper & Floresco, 2011; Stopper et al., 2012), an increase in the probability of receiving the uncertain outcome produced an increase in uncertain choices.

Furthermore, these results also demonstrated that increases in the magnitude of the U-S outcome resulted in an increase in uncertain choices.

To determine whether the effect of the U-S reward magnitude on choice behavior was not simply due to the different expected values at each probability of uncertain food delivery, the choice results were plotted as a function of the uncertain expected value in the bottom panel of Figure 2.1. This shows the same general trend as seen in the top panel of Figure 2.1; that is, at similar expected values of the uncertain choice, the rats in Group 1-11 chose the uncertain outcome less than the rats in Group 2-11, which chose the uncertain outcome less than those in Group 4-11. According to normative/rational theories of choice behavior, the rats in Group 1-11 were behaving irrationally, avoiding the uncertain choice despite the potential to earn considerably more food at higher probabilities; however, previous research has indeed shown that animals do not make choices in accordance with such normative theories (see Kalenscher & van Wingerden, 2011). Thus, the apparent group differences in choice behavior did not purely reflect differences in expected value across probabilities of uncertain food delivery, but rather a strong effect of the magnitude of the U-S reward, with groups receiving a greater U-S reward magnitude making uncertain choices more often. Accordingly, the cost of a small outcome following an uncertain choice may have outweighed the benefit of receiving the larger outcome. Therefore, while the rats did demonstrate sensitivity to expected value, as indicated by a general increase in uncertain choice behavior with increases in the probability of uncertain food, the corresponding behavior appeared to be more dependent on the individual outcomes of choices rather than the expected value of the choice.

Molecular analysis

Figure 2.2 shows the log odds of an uncertain choice following each possible outcome of the previous trial as a function of the probability of uncertain food delivery. Overall, the rats in Group 4-11 were most likely to make an uncertain choice following all outcomes. Additionally, all groups showed a general propensity to make more uncertain choices following uncertain-food outcomes and to make more certain choices following certain-small (C-S) and certain-large (C-L) outcomes, indicative of win-stay / lose-shift behavior. In several circumstances, the propensity to make an uncertain choice following each outcome was affected by the probability of uncertain food delivery, suggesting that the degree of win-stay / lose-shift behavior was moderated by the probability of "winning" for an uncertain choice (see Marshall & Kirkpatrick, 2013); for example, the rats in Groups 1-11 and 2-11 made more certain than uncertain choices following uncertain-zero (U-Z) outcomes at lower probabilities of uncertain food but vice versa at greater probabilities of uncertain food delivery. Interestingly, relative to that of Groups 1-11 and 2-11, the choice behavior in Group 4-11 following U-S and uncertain-large (U-L) outcomes seemed more similar, potentially suggesting a more comparable treatment of the two uncertain food outcomes in this group relative to that in Groups 1-11 and 2-11.

The conditionality of the analysis of the choice behavior given the previous outcome is problematic under the circumstances that a particular previous outcome may never be delivered; for example, if an animal never makes an uncertain choice, then there will be no choice data given uncertain outcomes in the previous trial, resulting in missing data for this experimental condition. Specifically, of the 840 data points involved in this analysis (24 subjects × 7 probabilities of uncertain food × 5 outcomes), there were 51 missing data points (approximately 6% of the data). Twenty-five of these 51 missing data points were due to missing data following U-S and U-L outcomes when the probability of uncertain food was .1 and the number of uncertain choices was relatively small. Due to such missing data in the current analysis, these conditional data were collapsed across probability (Figure 2.3); of the 120 data points that resulted from collapsing across probability (24 subjects × 5 outcomes), there were no missing data points. Following C-S and C-L outcomes, the rats were more likely to stay on the certain side than they were to switch to the uncertain side. Following U-Z, U-S, and U-L outcomes, the rats were more likely to make another uncertain choice. An ANOVA with previous outcome as the within groups factor and U-S reward magnitude group as the between groups factor revealed main effects of previous outcome, $F(4, 84) = 224.85$, $p < .001$, and group, $F(2, 21) = 9.78$, $p = .001$, but no Previous Outcome × Group interaction, $F(8, 84) = 1.45$, $p = .189$. As subsequent post hoc analyses were performed to evaluate both the main effects of group and previous outcome, these post hoc comparisons employed a Bonferroni correction in order to provide a more conservative test for evaluating these effects along multiple dimensions. These comparisons revealed that Group 1-11 chose the uncertain outcome significantly less than both Groups 2-11 and 4-11, $p < .05$, and that Groups 2-11 and 4-11 did not significantly differ in regards to their post outcome choice behavior, $p > .05$. Furthermore, choice behavior following C-S and C-L outcomes was significantly less than that following U-Z, U-S, and U-L outcomes, $p < .05$, and that choice behavior following U-Z outcomes was significantly less than that following U-S and U-L outcomes, $p < .05$. Choice behavior following C-S and C-L outcomes and following U-S and U-L outcomes did not significantly differ, $p > .05$. Therefore, these results suggest that the rats did not differentiate the smaller and larger food outcomes of each choice in regards to subsequent choice behavior, but rather adjusted their subsequent choice behavior on the conditions of whether or not they were rewarded for a previous choice; such results support the possibility that gains and losses were differentiated depending on whether the corresponding magnitudes are greater than or equal to zero (i.e., a zero-based reference point), respectively.

Previous research has also shown similar choice behavior following outcomes of different magnitudes of the same choice (Marshall & Kirkpatrick, 2013). Therefore, in conjunction with the present results, the effects of the previous outcome (or lack of) on subsequent choice behavior may reflect some dependence on the reception rather than the magnitude of reward. As such, gains and losses may be encoded relative to a zero-based reference point rather than the expected values of either choice. Such an explanation would predict that the rats may show similar choice behavior following outcomes of similar magnitudes, regardless of the choice that leads to such outcomes. Accordingly, Figure 2.4 shows the log odds of staying with the same choice following the two-pellet C-S and U-S outcomes in Group 2-11 and the four-pellet C-L and U-S outcomes in Group 4-11; there were no cases of missing data for this analysis. The log odds of staying, rather than the log odds of uncertain choices, was analyzed here because the rats would be predicted to show similar win-stay / lose-shift behavior if both outcomes were treated as equivalent gains relative to the same reference point (i.e., a zero-based reference point). Group 2-11 appeared to show a slight decrease in the log odds of staying following U-S outcomes relative to C-S outcomes, and Group 4-11 showed a slight increase in the log odds of staying following U-S outcomes relative to C-L outcomes. Paired-sample *t*-tests revealed that Group 2-11 did not show significant differences in choice behavior following C-S and U-S outcomes, $t(7) = 1.00$, $p = .351$, and that Group 4-11 did not show significant differences in choice behavior following C-L and U-S outcomes, $t(7) = 1.48$, $p = .181$. Therefore, these results potentially suggest that gains and losses may have been regarded as such relative to a zero-based reference point. However, this same hypothesis also seems to suggest that the groups should not have differed to the extent that they did, as each group would have been exposed to relatively comparable gains and losses. Therefore, a zero-based reference point may not have served as the reference point. Accordingly, even though reward omission is a critical determinant of post-outcome behavior (e.g., Marshall & Kirkpatrick, 2013; also see Amsel & Roussel, 1952; Staddon & Innis, 1966), it is possible that gains and losses were being distinguished given a different reference point and that reward omission simply served as a greater loss.

In conjunction with our hypotheses and specific goals concerning the distinction of gains from losses, additional analyses were performed to determine if there were group differences in regards to choice behavior specifically following U-S and U-L outcomes. A presence of significant differences between choice behaviors following U-S and U-L outcomes may then suggest that such outcomes were regarded as losses and gains, respectively, and that the group differences were due to these differential gains and losses. A repeated measures ANOVA with previous outcome (U-S, U-L) as the within groups factor and U-S reward magnitude group as the between groups factor revealed a significant increase in the log odds of an uncertain choice following U-L relative to U-S outcomes, $F(1, 21) = 7.79$, $p = .011$, a main effect of group, $F(2, 21) = 4.23$, $p = .029$, and a Previous Outcome × Group interaction, $F(2, 21) = 5.37$, $p = .013$. Post hoc Tukey comparisons indicated that Groups 1-11 and 2-11 were significantly less likely to make an uncertain choice following U-S outcomes than following U-L outcomes, ps < .05; the difference in choice behavior following U-S and U-L outcomes was not significant for Group 4-11, $p > .05$. Furthermore, additional post hoc Tukey comparisons revealed significant differences across all groups regarding uncertain choice following U-S outcomes, and that Group 1-11 made significantly fewer uncertain choices following U-L outcomes compared to that of

Groups 2-11 and 4-11. Therefore, these analyses suggest that the outcome magnitude of a previous uncertain choice did elicit differential subsequent choice behavior. Such differential behavior may have been due to the U-S and U-L outcomes being regarded as uncertain losses and gains, respectively, specifically in Groups 1-11 and 2-11, suggesting that the reference point may be located between the magnitudes of these groups' U-S outcomes (1 and 2 pellets) and the magnitude of Group 4-11's U-S outcome (4 pellets).

As described above, uncertain gains and losses may be distinguished by whether they are greater than or equal to zero (zero-based reference point), greater than or less than the expected value of the uncertain choice (uncertain-choice-based reference point), or greater than or less than the expected value of the alternative certain choice (certain-choice-based reference point). The more targeted analysis of choice behavior following U-S and U-L outcomes supports the latter; as the expected value of the certain choice was constant, the uncertain-outcome magnitudes were consistently either greater than or less than the expected value of the certain choice. Therefore, the significant differences between U-S and U-L outcomes with absolute magnitudes less than and greater than the expected value of the certain choice, respectively, appear to suggest the certain-choice-based reference point as the reference point for uncertain gains and losses. However, as there were group differences in the magnitudes of the uncertain food rewards, there were also group differences in the expected value of the uncertain choice. The U-S outcome was greater than the expected value of the uncertain choice in one, two, and four probability-of-uncertain-food conditions for Groups 1-11, 2-11, and 4-11, respectively (see Table 2.1). Accordingly, the significant differences (or lack of) between U-S and U-L outcomes may have reflected the corresponding reward magnitudes being less than and greater than the expected value of the uncertain choice, respectively, rather than less than and greater than the expected value of the certain choice. If so, then the rats should have showed differences between post U-L and post U-S choice behavior dependent on the relationship between such outcomes and the expected value of the uncertain choice. Figure 2.5 shows the difference score between post U-L and post U-S choice behavior as a function of the relationship between the U-S reward magnitude and the expected value of the uncertain choice; these difference scores were calculated by subtracting the log odds of an uncertain choice following U-S outcomes from that following U-L outcomes for each probability (i.e., the data in the right two panels of Figure 2.2). Of the 168 data points involved in this analysis (24 subjects × 7 expected values of uncertain food), there were 31 missing data points; twenty of these 31 missing data points were due to the absence of data following either U-S or U-L outcomes at probabilities of uncertain food .1 and .25, in which the number of total uncertain choices (and thereby the total number of U-S and U-L outcomes) was relatively small. As seen in Figure 2.5, there were no apparent effects of the U-S reward magnitude as a gain or a loss relative to the expected value of the uncertain choice on subsequent choice behavior. However, the general tendency to make more uncertain choices following U-L outcomes than following U-S outcomes in Groups 1-11 and 2-11, but not in Group 4-11, does support an explanation of a certain-choice-based reference point serving as a reference point for uncertain gains and losses. Accordingly, uncertain outcomes that are less than (greater than) the expected value of the certain choice would be encoded as losses (gains), resulting in a decreased (increased) tendency to make a subsequent uncertain choice. Furthermore, if this local tendency to stay following uncertain gains and switch following uncertain losses was collapsed across trials, such that a higher frequency of gains produced more uncertain choices and a higher frequency of losses produced more certain choices, then such local behavior may ultimately result in the global pattern of an increase in uncertain-choice behavior as a function of the probability of uncertain food delivery (see Kacelnik, Vasconcelos, Monteiro, & Aw, 2011).

Given the significant differences in uncertain-choice behavior following U-Z and U-S outcomes in all groups, and following U-S and U-L outcomes in Groups 1-11 and 2-11, the present results also potentially suggest that rats are more sensitive to a relative loss versus a relative gain (see Kahneman & Tversky, 1979; Tversky & Kahneman, 1981, 1991). In all groups, the absolute difference between the U-Z and U-S outcomes was objectively smaller than the absolute difference between U-S and U-L outcomes; however, while Groups 1-11 and 2-11 showed significantly different choice behavior following U-Z and U-S outcomes despite this relatively small absolute difference in magnitude, Group 4-11 showed relatively similar choice behavior following U-S and U-L outcomes despite this relatively larger absolute difference in magnitude. The absence of a significant difference between choice behaviors following U-S and U-L outcomes in Group 4-11 may then suggest that as long as the outcome of a successful "gamble" (i.e., an uncertain choice) is greater than the certain choice's expected value, then subsequent uncertain choice behavior will be less affected by the outcome magnitude of a previous gamble, compared to if the outcome of a successful gamble is smaller in magnitude than the certain choice's expected value. Accordingly, this differential sensitivity to the magnitude of the uncertain outcomes, dependent on how such outcomes compare to the value of the certain choice, may indeed reflect a differential sensitivity to relative gains versus relative losses (see Kahneman & Tversky, 1979; Tversky & Kahneman, 1981, 1991). Therefore, these results advance our understanding of the trial-by-trial mechanisms of probabilistic choice behavior in animals; the degree of an uncertain loss relative to the alternative certain choice may have impacted subsequent choice behavior more than the degree of an uncertain gain.

Table 2.1 Probability of food for an uncertain choice for each group in Experiment 1 that received different pellet amounts following a rewarded uncertain choice and for each subgroup that received different orders of probabilities of uncertain food delivery. Group 1-11 received 1 or 11 pellets following an uncertain choice, Group 2-11, 2 or 11 pellets, and Group 4-11, 4 or 11 pellets. The overall expected value of the uncertain choice is included in parentheses.

	Order 1			Order 2		
Phase	Group 1-11	Group 2-11	Group 4-11	Group 1-11	Group 2-11	Group 4-11
1-2	.50 (**3**)	.50 (**3.25**)	.50 (**3.75**)	.50 (**3**)	.50 (**3.25**)	.50 (**3.75**)
3	.75 (**4.5**)	.75 (**4.875**)	.75 (**5.625**)	.25 (**1.5**)	.25 (**1.625**)	.25 (**1.875**)
4	.33 (**2**)	.33 (**2.17**)	.33 (**2.5**)	.67 (**4**)	.67 (**4.33**)	.67 (**5**)
5	.67 (**4**)	.67 (**4.33**)	.67 (**5**)	.33 (**2**)	.33 (**2.17**)	.33 (**2.5**)
6	.25 (**1.5**)	.25 (**1.625**)	.25 (**1.875**)	.75 (**4.5**)	.75 (**4.875**)	.75 (**5.625**)
7	.90 (**5.4**)	.90 (**5.85**)	.90 (**6.75**)	.10 (**0.6**)	.10 (**0.65**)	.10 (**0.75**)
8	.10 (**0.6**)	.10 (**0.65**)	.10 (**0.75**)	.90 (**5.4**)	.90 (**5.85**)	.90 (**6.75**)
9	.50 (**3**)	.50 (**3.25**)	.50 (**3.75**)	.50 (**3**)	.50 (**3.25**)	.50 (**3.75**)

Figure 2.1 Mean (±SEM) log odds of an uncertain choice for each group in Experiment 1 as a function of the probability of uncertain food delivery (top panel) and the expected value of an uncertain choice (bottom panel).

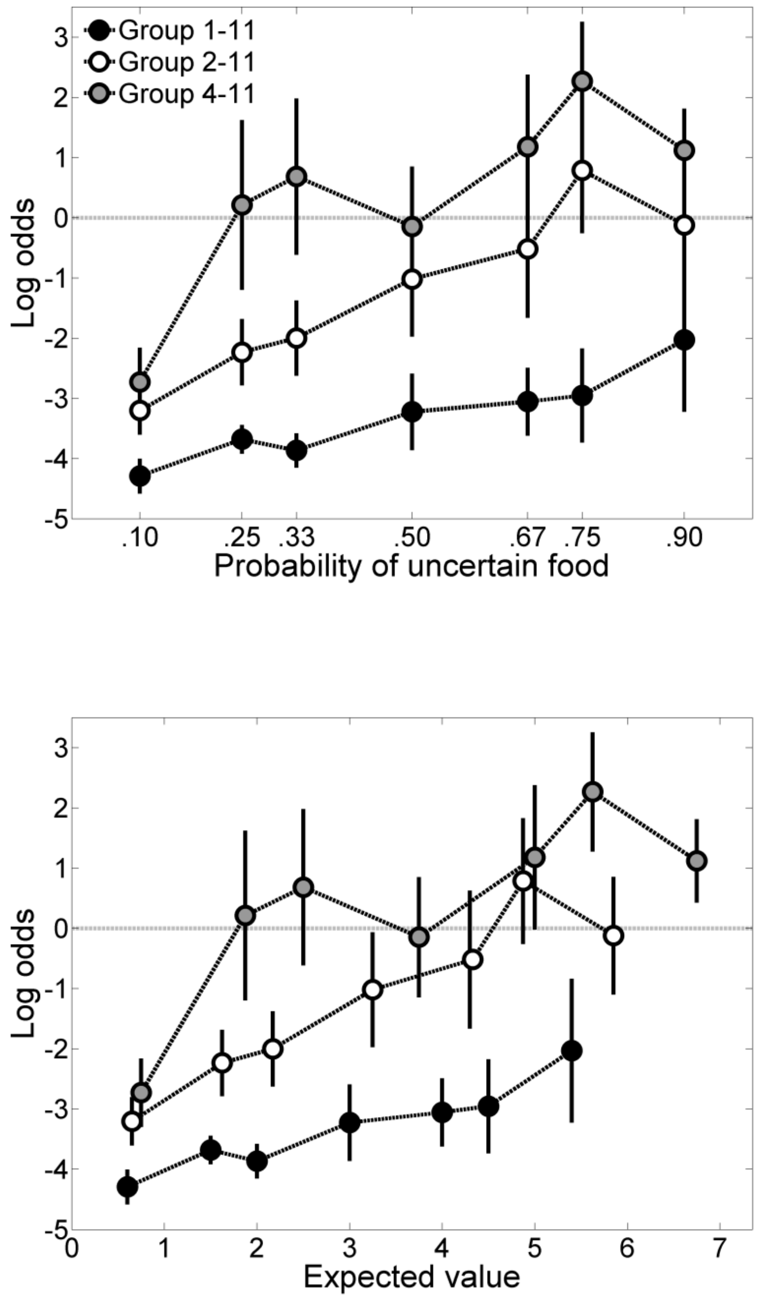


Figure 2.2 Mean (±SEM) log odds of an uncertain choice for each group in Experiment 1 as a function of both the outcome of the previous choice and the probability of uncertain food delivery. C-S = certain-small; C-L = certain-large; U-Z = uncertain-zero; U-S = uncertain-small; U-L = uncertain-large.

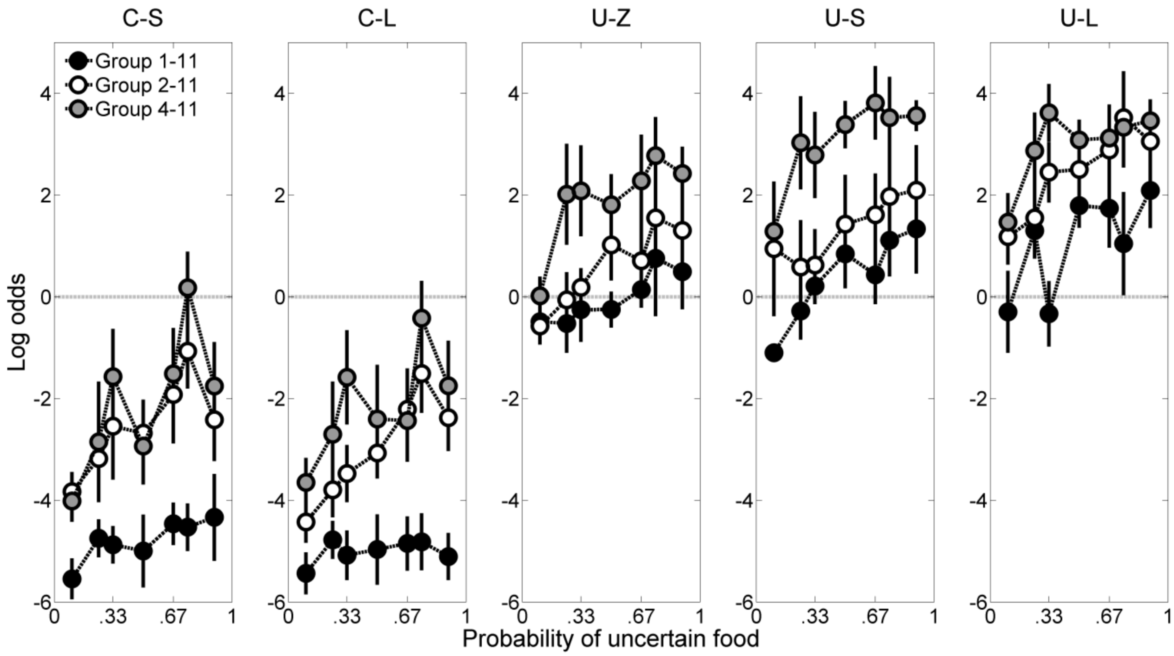


Figure 2.3 Mean (±SEM) log odds of an uncertain choice for each group in Experiment 1 as a function of the outcome of the previous choice, collapsed across the probability of uncertain food delivery. C-S = certain-small; C-L = certain-large; U-Z = uncertain-zero; U-S = uncertain-small; U-L = uncertain-large.

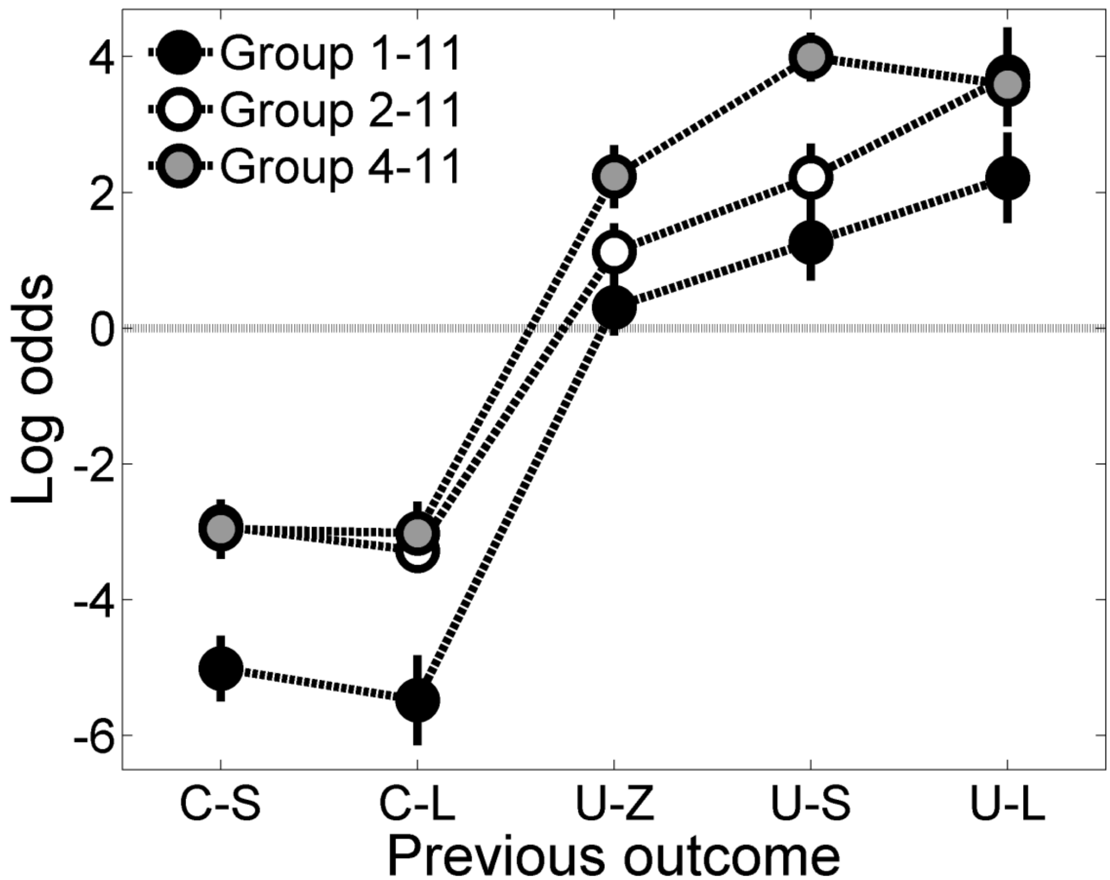


Figure 2.4 Mean (±SEM) log odds of staying on the same choice for Groups 2-11 and 4-11 in Experiment 1 as a function of the outcome of the previous choice, collapsed across the probability of uncertain food delivery. C-S = certain-small; C-L = certain-large; U-S = uncertain-small.

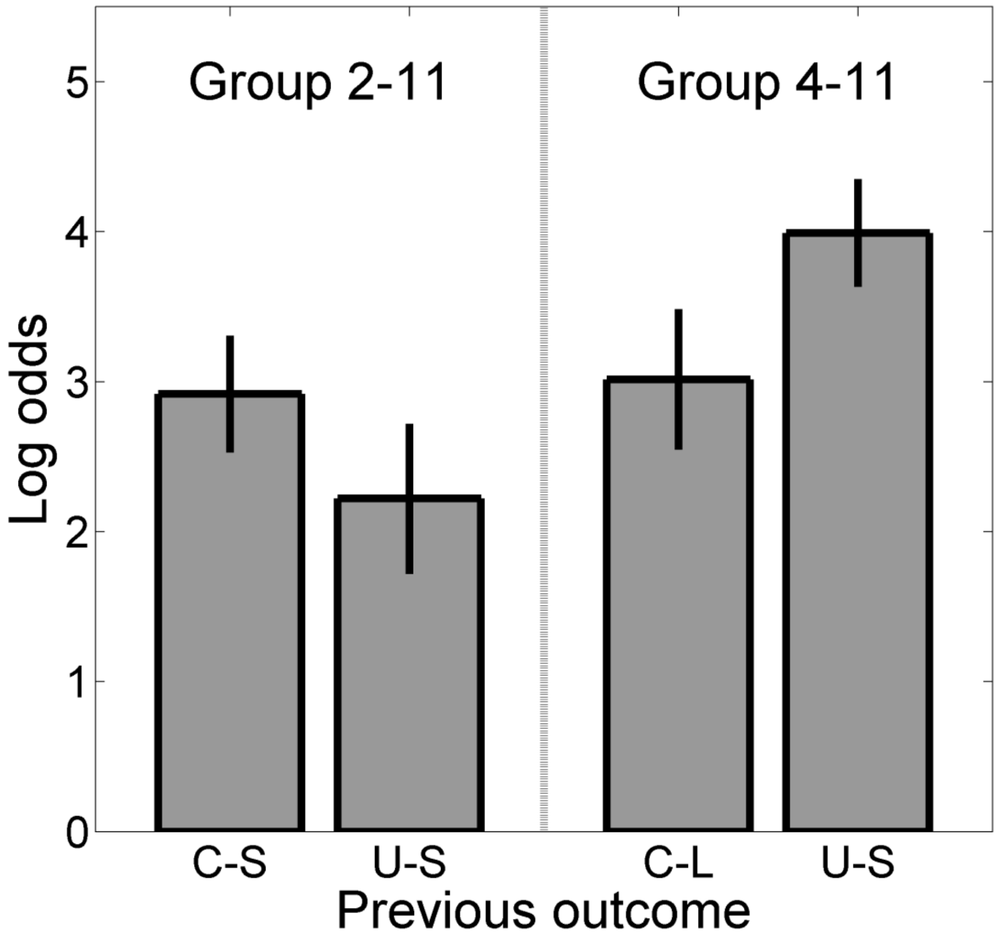
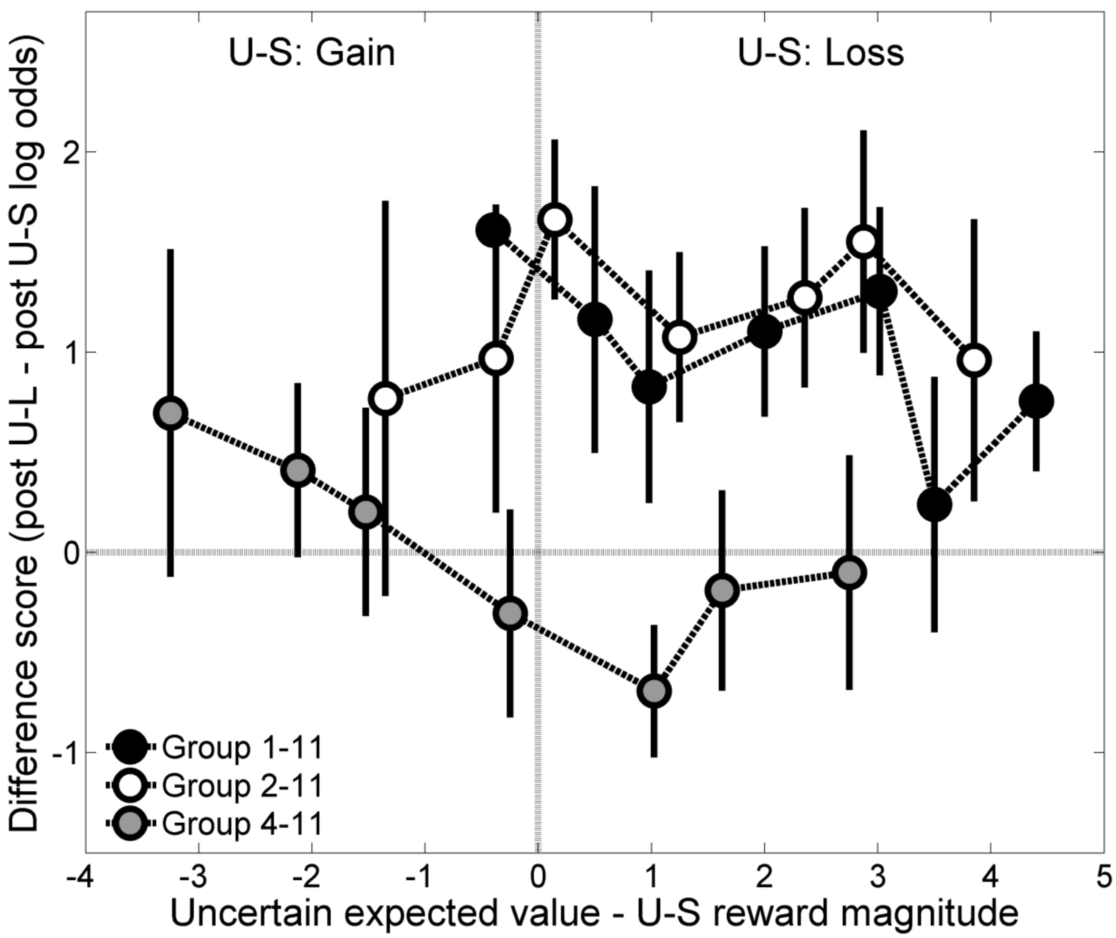


Figure 2.5 Mean (±SEM) difference score between the log odds of an uncertain choice following uncertain-large (U-L) outcomes and the log odds of an uncertain choice following uncertain-small (U-S) outcomes for each group in Experiment 1 as a function of the difference between the expected value of the uncertain choice and the absolute magnitude of the U-S outcome. A negative/positive difference on the abscissa indicates that the U-S outcome magnitude was greater than/less than the expected value of the uncertain choice. A negative/positive difference on the ordinate reflects a greater likelihood to make uncertain choices following U-S/U-L outcomes.



Chapter 3 - Experiment 2

The results from Experiment 1 suggested that the magnitude of a small uncertain (i.e., risky) outcome can affect overall and local choice behavior, and the degree to which it does appears to be dependent on its relationship to the certain alternatives in the environment. The results from Experiment 1 also suggested that the rats exhibited a differential sensitivity to uncertain gains and losses. Accordingly, these results suggest that while differential uncertain losses may have relatively large impacts on subsequent uncertain choice behavior, differential gains would cause little if any change in subsequent choice behavior. Accordingly, Experiment 2 was designed to elucidate the effects of differential gains on subsequent choice behavior, by manipulating the magnitude of the U-L outcome. If rats are more sensitive to relative losses than they are to relative gains, then groups that receive different outcome magnitudes following an uncertain choice should show little, if any, difference in choice behavior following the different U-L outcomes, because they are all gains relative to the expected value of the certain choice. However, as rats have been shown to be sensitive to reward magnitude, exhibiting increases in response rate as a result of increases in the magnitude of reward (e.g., Galtress & Kirkpatrick, 2010), an alternative explanation of the results from Experiment 1 is that the significant difference in choice behavior following U-S and U-L outcomes in Groups 1-11 and 2-11, but not in Group 4-11, may have been due to increased discriminability between the U-S and U-L outcomes. Therefore, if the rats' subsequent choice behavior is more dependent on the discriminability of the uncertain outcomes, then there should be an increasing difference between post U-S and post U-L uncertain choice behavior with increasing separation of U-S and U-L outcome magnitudes.

Method

Animals

Twenty-four experimentally naïve rats, approximately 45 days of age at arrival, served as subjects. The housing and husbandry conditions were identical to Experiment 1, with the exception that the colony room lights turned off at 8 am.

Apparatus

The experimental apparatus was identical to Experiment 1.

Procedure

Pre-training

The pre-training procedure was identical to Experiment 1.

Training

Training was identical to Experiment 1 with the following exceptions. In this experiment (see Table 3.1), the U-L reward magnitude was 6, 9 or 11 pellets in Groups, 4-6, 4-9, and 4-11, respectively, while the U-S magnitude was maintained at 4 pellets. The probabilities of uncertain food delivery were .10, .33, .50, .67 and .90 (see Table 3.1). Phases 1 and 2 involved a probability of uncertain food delivery of .50, with a reversal of lever assignments occurring in Phase 2. The two orders of uncertain food probabilities for Phases 3-6 were .90, .33, .67, .10 (Order 1), and .10, .67, .33, .90 (Order 2); additionally, as in Experiment 1, assignment of the rats within each group to the two orders depended on their mean choice behavior in Phase 2. In Phase 7, all rats were returned to the probability of .50. Phases 1 and 2 lasted for 20 sessions each, and Phases 3-7 lasted for 10 sessions each. Sessions terminated following the completion of 100 free choice trials per session or after approximately 2 hr, whichever occurred first.

Data analysis

Data analysis was the same as in Experiment 1, and Phase 7 was used for analysis of the .50 probability for all rats.

Results and Discussion

Molar analysis

The top panel of Figure 3.1 shows the log odds of an uncertain choice as a function of the probability of uncertain food delivery. All groups showed a general increase in uncertain choices as a function of the probability of uncertain reward, but there were no systematic group differences. An ANOVA with probability as the within groups factor and U-L reward magnitude group as the between groups factor revealed a main effect of probability, $F(4, 84) = 22.64$, $p < .001$, but no effect of group, $F(2, 21) = .116$, $p = .891$, and no Probability × Group interaction, $F(8, 84) = .559$, $p = .808$. Post hoc Tukey comparisons revealed significant differences in uncertain choices across all but two pairwise comparisons, $p < .05$: .10 versus .33 and .50 versus .67. Therefore, as shown previously (Cardinal & Howes, 2005; Marshall & Kirkpatrick, 2013; Mazur, 1988; Mobini et al., 2002; St. Onge et al., 2012; Stopper & Floresco, 2011; Stopper et al., 2012), an increase in the probability of uncertain food delivery produced a general increase in uncertain choices. However, in contrast to the effects on choice behavior of different U-S reward magnitudes (see Experiment 1), these results indicate changes in the magnitude of the U-L outcome did not considerably affect uncertain choices (but see Hayden, Heilbronner, Nair, & Platt, 2008).

As a means to further explore this absence of an effect of U-L outcome magnitude on choice behavior, the bottom panel of Figure 3.1 shows the log odds of uncertain choices as a function of the expected value of the uncertain choice. While each group showed an increase in uncertain choice behavior with increases in the expected value of the uncertain choice, the similar expected values of the uncertain choice across groups elicited relatively different patterns of uncertain choice behavior. Therefore, similar to the results of Experiment 1, the expected value of the uncertain choice did not appear to be the only factor driving uncertain choice behavior. Rather, if both uncertain-food outcomes for the groups were regarded as gains relative to the expected value of the certain choice, and if the animals exhibited a reduced sensitivity to such differential gains, as described above, then minimal group differences would be expected (Figure 3.1, top panel). Therefore, the present results support the explanations of the results in Experiment 1.

Molecular analysis

Figure 3.2 shows the log odds of uncertain choices as a function of the probability of uncertain food delivery following each of the five possible outcomes of the previous choice. Following each outcome, all groups showed a general increase in uncertain choices as the probability of uncertain food increased. No systematic group differences were apparent. Following C-S and C-L outcomes, the groups tended to make another certain choice; following U-S and U-L outcomes, the groups tended to make another uncertain choice. At higher probabilities of uncertain food delivery, the groups tended to stay on the uncertain side following U-Z outcomes, but to switch to the certain side when at the lower probabilities of uncertain food delivery. Thus, as shown previously (Marshall & Kirkpatrick, 2013), the rate of win-stay / lose-shift behavior depended on the previous outcome as well as the probability of uncertain food delivery.

As done in Experiment 1, the data shown in Figure 3.2 were collapsed across the probability of uncertain food delivery. Of the 600 data points within the data shown in Figure

3.2 (24 subjects × 5 probabilities of uncertain food × 5 outcomes), there were 23 missing data points (approximately 3.8% of these data). Seventeen of these 23 missing data points were due to missing data following U-S and U-L outcomes when the probability of uncertain food was .1 and the number of uncertain choices was relatively small. Figure 3.3 shows the effects of the previous outcome on subsequent choice behavior, collapsed across probability; of the 120 data points that resulted from collapsing across probability (24 subjects × 5 outcomes), there were no missing data points. The groups were more likely to make certain choices following certain outcomes, and uncertain choices following uncertain outcomes. Additionally, all groups showed an increased tendency to make uncertain choices following U-S and U-L outcomes than following U-Z outcomes (i.e., win-stay / lose-shift behavior); furthermore, there was a slight decrease in subsequent uncertain choice behavior following C-L outcomes compared to C-S outcomes. An ANOVA with previous outcome as the within groups factor and U-L reward magnitude group as the between groups factor revealed a main effect of previous outcome, $F(4, 84) = 295.69$, $p < .001$, no effect of U-L reward magnitude, $F(2, 21) = .06$, $p = .942$, and a Previous Outcome × Group interaction, $F(8, 84) = 2.16$, $p = .039$. Simple-effects analyses (using a one-way ANOVA) with U-L reward magnitude as the between groups factor were conducted on the log odds of an uncertain choice following each outcome; such simple effects analyses were employed here in order to specifically evaluate the effects of group on choice behavior following individual outcomes without the error provided by other post-outcome choice behavior affecting such analyses. These analyses did not reveal a main effect of group following any of the previous outcomes, $Fs(2, 21) < 2.1$, $ps > .15$. Therefore, different U-L reward magnitudes across groups did not appear to systematically affect either global or local choice behavior. Additional post hoc Tukey comparisons were conducted to evaluate the main effect of previous outcome. These analyses revealed that the rats exhibited a significant reduction in the log odds of an uncertain choice following C-S and C-L outcomes than following U-Z, U-S, and U-L outcomes, $p < .05$, and a significant reduction in the log odds of an uncertain choice following U-Z outcomes than following U-S and U-L outcomes, $p < .05$. However, there were no significant differences in the log odds of an uncertain choice following C-S and C-L outcomes and following U-S and U-L outcomes, $p > .05$. Therefore, similar to that shown in Experiment 1 and previously (e.g., Marshall & Kirkpatrick, 2013; St. Onge et al., 2012; Stopper & Floresco, 2011), there was an increase in the tendency to make uncertain choices following uncertain-food outcomes compared to that following U-Z outcomes, indicative of win-stay / lose-shift behavior.

To address the hypothesis that rats exhibit differential sensitivity to uncertain gains and losses relative to a certain-choice-based reference point, additional analyses were performed to determine if there were differences in choice behavior following U-S and U-L outcomes as done in Experiment 1. A repeated measures ANOVA with previous outcome (U-S, U-L) as the within groups factor and U-L reward magnitude group as the between groups factor did not reveal any significant effects: previous outcome, $F(1, 21) = .28$, $p = .602$, group, $F(2, 21) = 1.40$, $p = .268$, Previous Outcome × Group, $F(2, 21) = .23$, $p = .795$. Therefore, these comparisons indicated that the groups did not exhibit significantly different choice behavior following U-S and U-L outcomes. Such results do not support an explanation in terms of the discriminability of the uncertain-food outcomes, which should have produced an increasing difference in choice behavior following U-S and U-L outcomes as a function of the difference between the uncertain outcome magnitudes. However, these results do support an explanation concerning the certain-choice-based reference point as the reference point for uncertain gains and losses; the absence of a significant difference between choice behaviors following U-S and U-L outcomes potentially suggests that both are treated as gains and that the rats exhibited a reduced sensitivity to the difference between such gains relative to that of differential losses (see Experiment 1).

The significant decreases in choice behavior following U-Z outcomes compared to uncertain food outcomes appear to suggest that U-Z outcomes were encoded as losses and uncertain food outcomes as gains. Therefore, in conjunction with the results and discussion from Experiment 1, the present data suggest that the certain-choice-based reference point served as the reference point distinguishing uncertain gains and losses. Additional support for this hypothesis is displayed in Figure 3.4, which shows the absolute difference between choice behavior following U-L and U-S outcomes as a function of the absolute difference between the expected value of the uncertain choice and the magnitude of the U-S outcome. Of the 120 data points involved in this analysis (24 subjects × 5 expected values of uncertain food), there were 16 missing data points; thirteen of these 16 missing data points were due to the absence of data following either U-S or U-L outcomes at probabilities of uncertain food .1, in which the number of total uncertain choices (and thereby the total number of U-S and U-L outcomes) was relatively small. The tendency for the functions to approximate zero difference suggests that there was little, if any, difference in choice behavior following the uncertain-food outcomes across conditions in which the U-S outcome was greater or less than the expected value of the uncertain choice. Therefore, uncertain gains and losses do not appear to have been gauged relative to the expected value of the uncertain choice (i.e., an uncertain-choice-based reference point). Furthermore, while it was suggested in Experiment 1 that the zero-based reference point may not serve as a reference point and that reward omission may actually reflect the greatest loss, the present data do not conclusively eliminate a zero-based reference point as a possible reference point. Figure 3.5 shows the log odds of staying on a choice following the four-pellet C-L and U-

S outcomes for each group; there were no cases of missing data in this analysis. Paired-sample *t*-tests indicated that the groups did not show significant differences in the log odds of staying on a certain or uncertain choice following C-L and U-S outcomes, respectively, $ts(7) < .65$, $ps > .540$. However, of the candidate reference points, the current data in conjunction with those of Experiment 1 appear to suggest that a certain-choice based reference point served to distinguish uncertain gains from uncertain losses. Furthermore, the absence of significant differences between choice behavior following U-S and U-L outcomes across groups in the present experiment suggests that the rats exhibited a relatively reduced sensitivity to differential gains.

Table 3.1 Probability of food for an uncertain choice for each group in Experiment 2 that received different pellet amounts following a rewarded uncertain choice and for each subgroup that received different orders of probabilities of uncertain food delivery. Group 4-6 received 4 or 6 pellets following an uncertain choice, Group 4-9, 4 or 9 pellets, and Group 4-11, 4 or 11 pellets. The overall expected value of the uncertain choice is included in parentheses.

	Order 1			Order 2		
Phase	Group 4-6	Group 4-9	Group 4-11	Group 4-6	Group 4-9	Group 4-11
1-2	.50 (**2.5**)	.50 (**3.25**)	.50 (**3.75**)	.50 (**2.5**)	.50 (**3.25**)	.50 (**3.75**)
3	.90 (**4.5**)	.90 (**5.85**)	.90 (**6.75**)	.10 (**0.5**)	.10 (**0.65**)	.10 (**0.75**)
4	.33 (**1.65**)	.33 (**2.145**)	.33 (**2.475**)	.67 (**3.35**)	.67 (**4.355**)	.67 (**5.025**)
5	.67 (**3.35**)	.67 (**4.355**)	.67 (**5.025**)	.33 (**1.65**)	.33 (**2.145**)	.33 (**2.475**)
6	.10 (**0.5**)	.10 (**0.65**)	.10 (**0.75**)	.90 (**4.5**)	.90 (**5.85**)	.90 (**6.75**)
7	.50 (**2.5**)	.50 (**3.25**)	.50 (**3.75**)	.50 (**2.5**)	.50 (**3.25**)	.50 (**3.75**)

Figure 3.1 Mean (±SEM) log odds of an uncertain choice for each group in Experiment 2 as a function of the probability of uncertain food delivery (top panel) and the expected value of an uncertain choice (bottom panel).

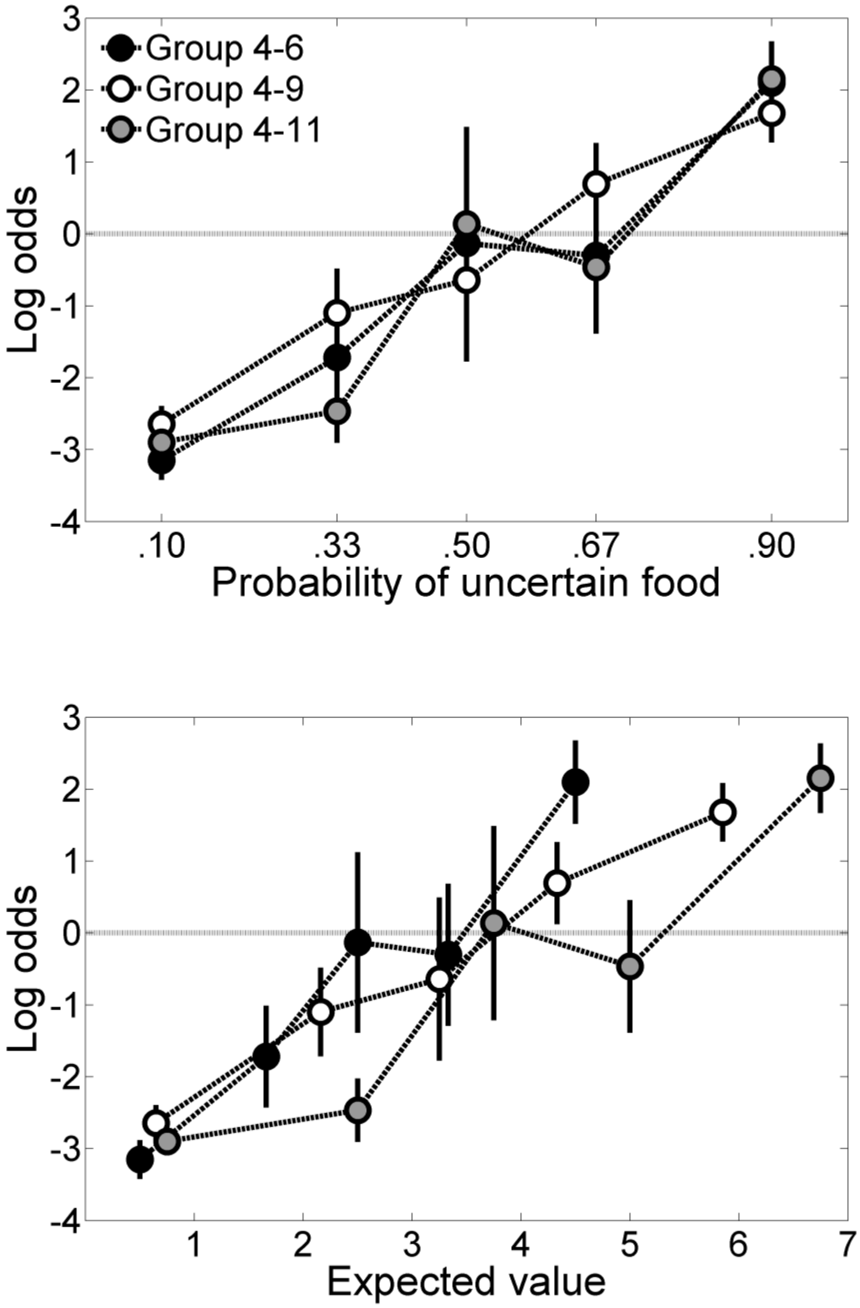


Figure 3.2 Mean (±SEM) log odds of an uncertain choice for each group in Experiment 2 as a function of both the outcome of the previous choice and the probability of uncertain food delivery. C-S = certain-small; C-L = certain-large; U-Z = uncertain-zero; U-S = uncertain-small; U-L = uncertain-large.

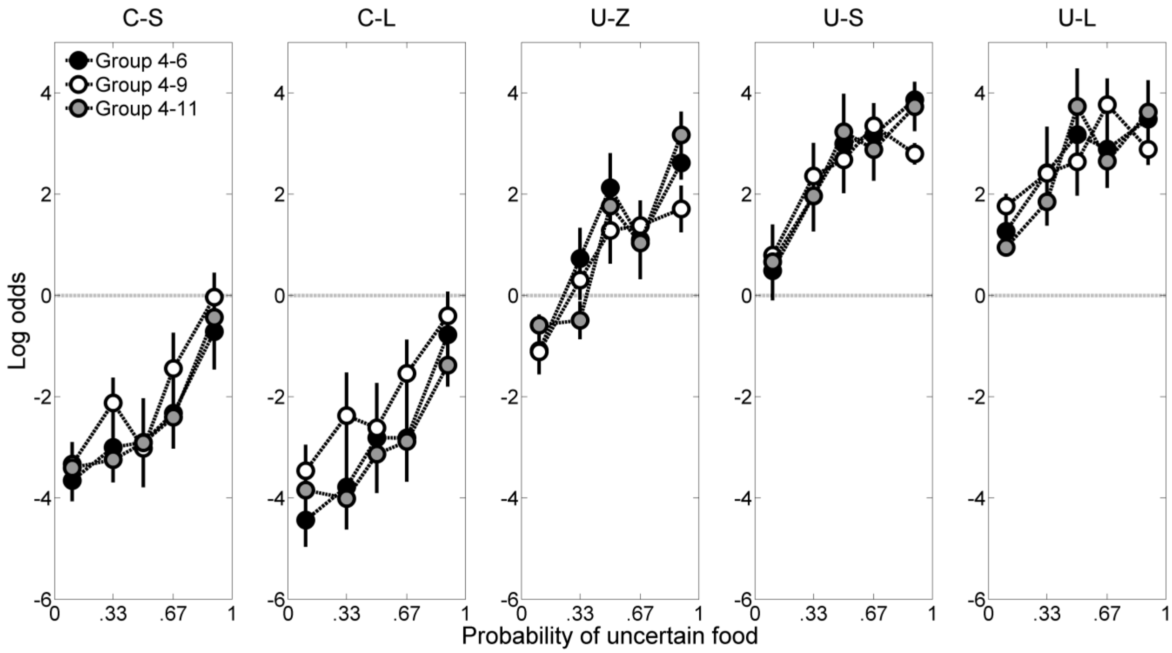


Figure 3.3 Mean (±SEM) log odds of an uncertain choice for each group in Experiment 2 as a function of the outcome of the previous choice, collapsed across the probability of uncertain food delivery. C-S = certain-small; C-L = certain-large; U-Z = uncertain-zero; U-S = uncertain-small; U-L = uncertain-large.

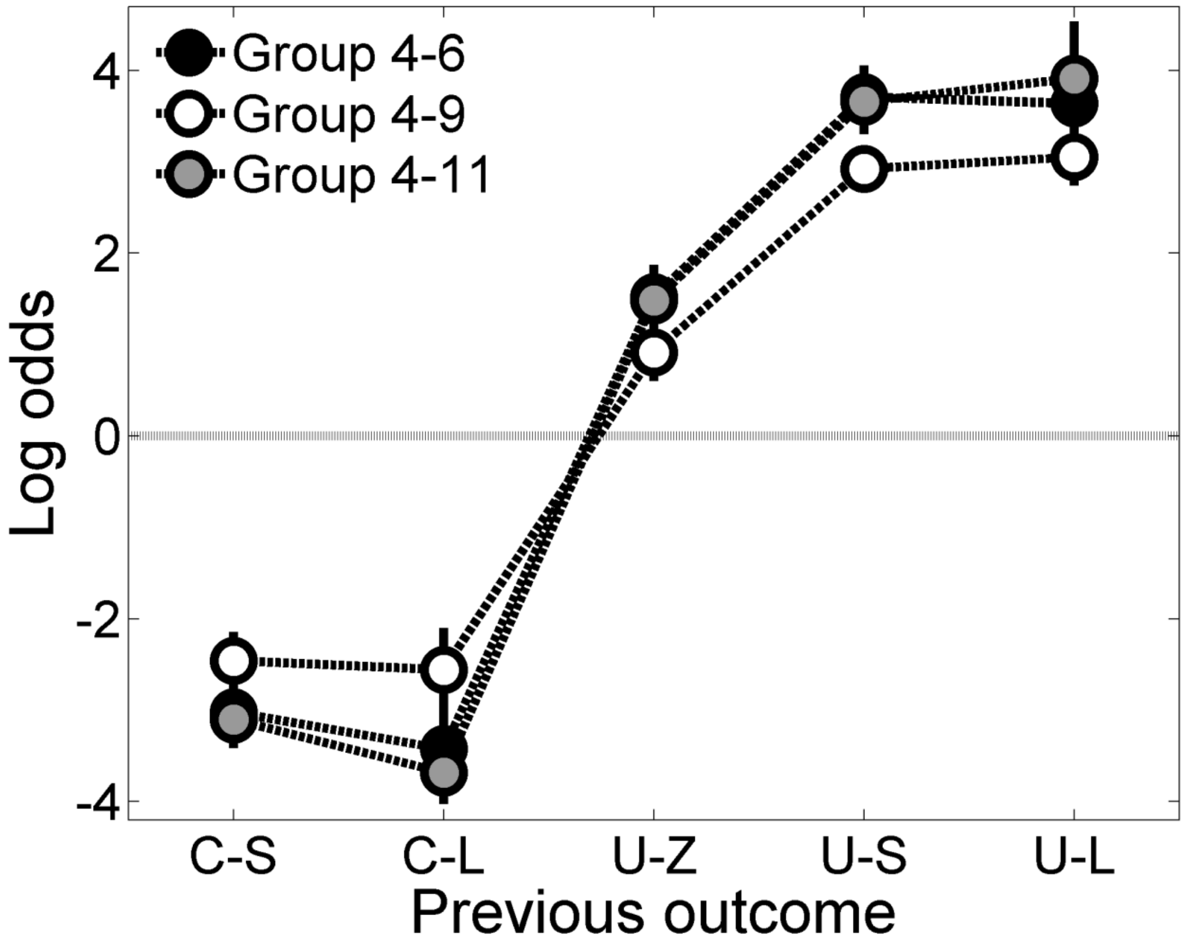


Figure 3.4 Mean (±SEM) difference score between the log odds of an uncertain choice following uncertain-large (U-L) outcomes and the log odds of an uncertain choice following uncertain-small (U-S) outcomes for all groups in Experiment 2 as a function of the difference between the expected value of the uncertain choice and the absolute magnitude of the U-S outcome. A negative/positive difference on the abscissa indicates that the U-S outcome magnitude was greater than/less than the expected value of the uncertain choice. A negative/positive difference on the ordinate reflects a greater likelihood to make uncertain choices following U-S/U-L outcomes.

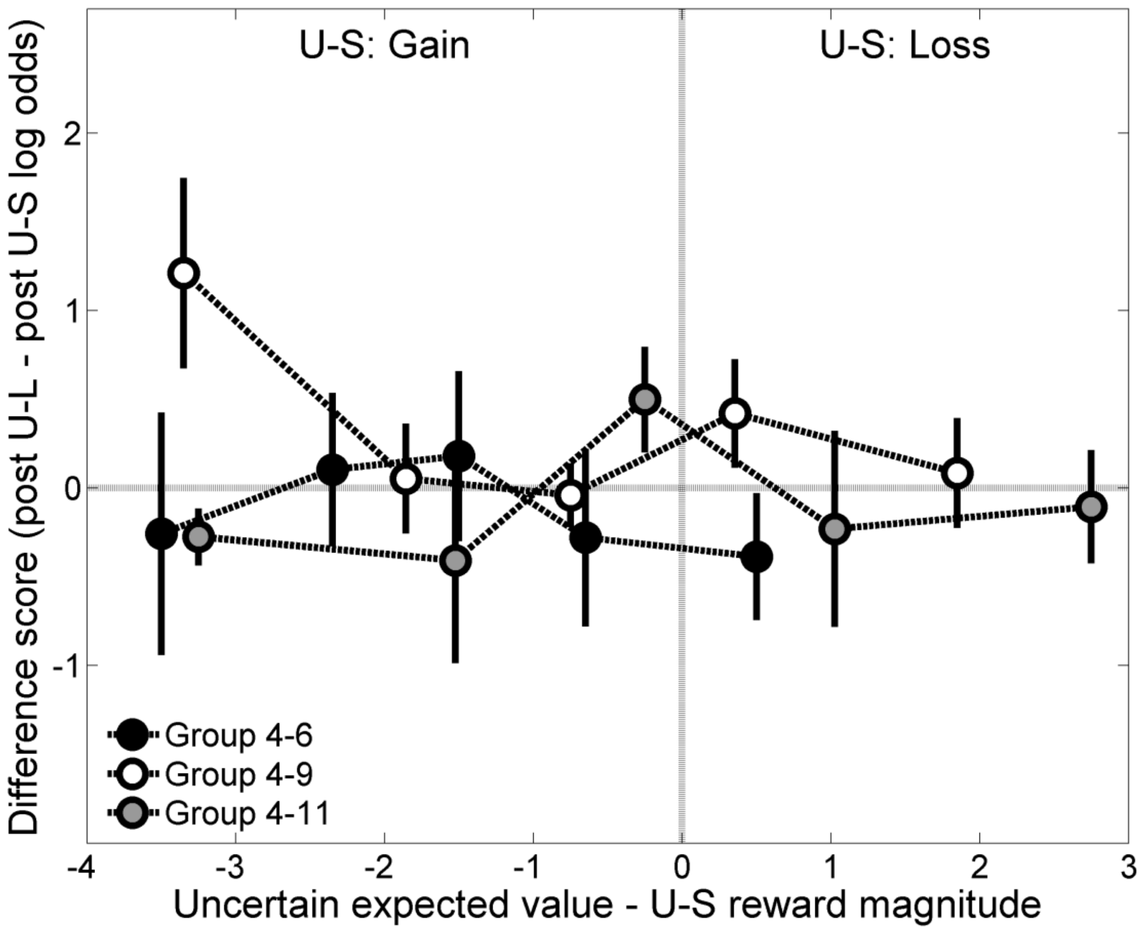
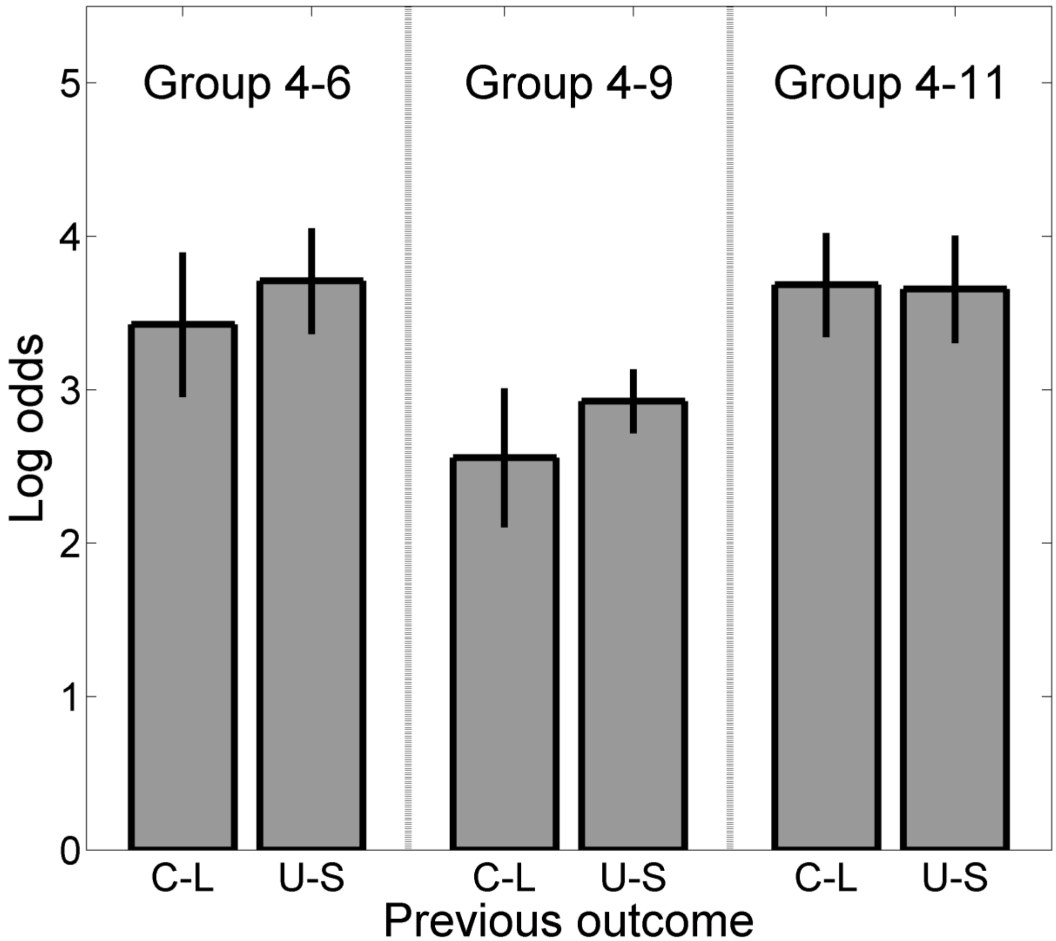


Figure 3.5 Mean (±SEM) log odds of staying on the same choice for each group in Experiment 2 as a function of the outcome of the previous choice, collapsed across the probability of uncertain food delivery. C-L = certain-large; U-S = uncertain-small.



Chapter 4 - General Discussion

An individual's decisions are considerably influenced by probabilistic gains and losses, whether they define the outcomes of upcoming decisions (e.g., Kahneman & Tversky, 1979; Levin, Schneider, & Gaeth, 1998) or the results of prior decisions (e.g., Gehring & Willoughby, 2002; Marshall & Kirkpatrick, 2013; St. Onge et al., 2012). While such effects are well-established, the reference point that partitions different outcomes as gains and losses is not. The human probabilistic choice literature has suggested that individuals' reference points reflect either their current state or a state of expectation or aspiration (Kahneman & Tversky, 1979; Hastie & Dawes, 2010; Tversky & Kahneman, 1981). Accordingly, different individuals may regard the same outcomes differently so that a gain for one individual may be a loss for another. In animals, it is less clear what distinguishes a gain from a loss. Such interspecies asymmetry discourages the ability to achieve a comprehensive understanding of the global and local effects of probabilistic gains and losses. For example, consider the use of consumable rewards in animal choice paradigms. Given the frequent use of monetary rewards in the human literature, the reduction in an individual's current monetary status due to a negative monetary outcome is more comprehensible than the reduction in the amount of food that an animal has already consumed, especially in consideration of the experimental methods in which humans may play with money that they have been provided rather than with their own. Accordingly, an analysis of gains and losses in animals must either employ reward magnitudes greater than or equal to zero, restricting the number of outcomes that may serve as gains and losses, or rather consider the amount of calories expended during each physical act of responding and whether the resulting reward does or does not compensate for such energy expenditure (i.e., gains and losses, respectively). Therefore, the different possibilities for reference points in animals may be more difficult to quantitatively distinguish and identify relative to those in humans. Accordingly, an analysis of prior gains and losses in probabilistic choice paradigms seems to require a more parametric design, as employed here, such that reference-point use in animals may be elucidated.

The primary goal of the present experiments was to determine the effects of uncertain rewards of different magnitudes on subsequent choice behavior. Such analyses may encounter possible concerns, such as in regards to the potential costs of switching between choices, which has been described previously in terms of animal choice behavior (see, e.g., Houston & McNamara, 1982; Krebs, Kacelnik, & Taylor, 1978), or the effects of satiety that may occur throughout an experimental session. However, as switching between choices (e.g., lose-shift) did not involve any experimenter-controlled costs within the present experiments, and as food delivery occurring between the two choice levers served as a means to center the animal between the levers prior to the next choice (i.e., equating any possible response costs involved in moving to one lever or the other), there did not appear to be any apparent costs that may have considerably impacted the present analysis. Furthermore, a strong effect of satiety would have been made evident had the groups receiving more food following uncertain choices made fewer uncertain choices, in accordance with the energy budget hypothesis (see Caraco, 1981; Houston & McNamara, 1982), as such groups would be expected to become sated earlier in an experimental session. Such an effect was not evident (Figures 2.3 and 3.3). Therefore, it is reasonable to interpret the present molecular data in terms of the previous outcome rather than primarily considering such absent costs and effects of satiety. Accordingly, previous research has shown that the previous outcome of a choice can influence subsequent choice behavior (e.g., Hayden & Platt, 2009; Marshall & Kirkpatrick, 2013; McCoy & Platt, 2005; Stopper & Floresco, 2011). However, to appropriately interpret such effects, it is important to consider whether such previous outcomes qualify as either gains or losses. As many probabilistic-choice tasks have lacked the parametric nature that would permit an understanding of reference points in animals, previous research has made such an understanding difficult to achieve. The present report initially discussed three possibilities for a reference point within probabilistic-choice task: a zero-based reference point, an uncertain-choice-based reference point, and a certain-choice-based reference point. These alternatives are all possible and indistinguishable given the traditional probabilistic-choice paradigms, in which probabilistic choices are followed by either the absences of reward (i.e., the U-Z) or larger rewards (i.e., the U-L), which are less than and greater than, respectively, the expected values of both the certain and uncertain choices. Given the behavioral and neural differences elicited by probabilistic gains and losses (e.g., Gehring & Willoughby, 2002; Kahneman & Tversky, 1979), it is therefore critical to determine which of these alternatives distinguishes gains from losses in animals, such that mechanisms underlying such behaviors can be determined.

Accordingly, the results of Experiments 1 and 2 suggest that the rats used the expected value of the alternative certain choice as a reference point for the uncertain gains and losses, and that they were more sensitive to differential losses than they were to differential gains (Figures 2.3 and 3.3). In regards to the former, the rats showed significant differences in choice behavior following uncertain outcomes greater than and less than the expected value of the certain choice (Figures 2.3 and 3.3), but did not show systematic differences in choice behavior following the U-S outcome depending on whether it was greater than or less than the expected value of the uncertain choice (Figures 2.5 and 3.4). Such results support a certain-choice-based reference point in contrast to an uncertain-choice-based reference point as the reference point for uncertain gains and losses. While these same results do not immediately disconfirm a zero-based reference point, the group differences (and lack of) in molar choice behavior from Experiments 1 and 2 may not support a zero-based reference point, as these differences may reflect the possibilities of prospective uncertain gains and losses. Recall that a zero-based reference point suggests that only U-Z outcomes are regarded as losses. However, the general risk-averse behavior in Group 1-11 (Experiment 1, Figure 2.1) may indicate that the one-pellet U-S outcome served as a relative loss given a certain-choice-based reference point rather than a relative gain given a zero-based reference point. A greater sensitivity to uncertain losses versus uncertain gains relative to a certain-choice-based reference point could have driven such behavior. Therefore, in accordance with the present results, uncertain choice outcomes increasingly less than the expected value of the certain choice may be regarded as having a subjectively larger influence than uncertain outcomes increasingly greater than the expected value of the certain choice (see Kahneman & Tversky, 1979; Tversky & Kahneman, 1981, 1991). Furthermore, given the constancy of the certain choice relative to dynamicity of the uncertain choice, the expected value of the certain choice may have served as the reference point for certain choice outcomes as well. The relative similarities in staying behavior following different choice outcomes of similar magnitudes would support this hypothesis (Figures 2.4 and 3.5), as outcomes being judged relative to the same reference point should seemingly produce similar switching versus staying behavior. Therefore, the results of Experiments 1 and 2 suggest that uncertain gains and losses were regarded as such relative to the expected value of the certain choice.

Theoretical approaches to probabilistic-choice behavior

Several theoretical frameworks of probabilistic choice have incorporated reference points in evaluating choice outcomes. While such frameworks have been frequently shown to account for molar choice behavior, the present focus will be on their abilities to account for choice behavior on a molecular scale. For example, two of the more influential theories of choice behavior are prospect theory (Kahneman & Tversky, 1979; Tversky & Kahneman, 1981) and optimal foraging theory (Stephens & Krebs, 1986). In prospect theory, gains and losses are gauged relative to an individual's subjective reference point, which may reflect what an individual currently has or rather what an individual expects or aspires to have; the value attributed to gains and losses is a negatively-accelerating function of the absolute difference between the corresponding outcome magnitudes and the reference point (Kahneman & Tversky, 1979). Furthermore, prospect theory predicts greater risk-seeking following losses (Kahneman & Tversky, 1979, p. 287; also see Gehring & Willoughby, 2002; Goyer et al., 2008; Riba et al., 2008; Tversky & Kahneman, 1981). In optimal foraging theory, an individual's choices are driven by the goal to maximize energy intake at the expense of the energy needed during the physical act of foraging (Stephens & Krebs, 1986, p. 8; also see Caraco, 1981; Rode, Cosmides, Hell, & Tooby, 1999; Stephens, 1981). Accordingly, the reference point for gains and losses is the minimum daily energy intake required for survival (also see Mishra & Fiddick, 2012; Mishra, Gregson, & Lalumière, 2012); if a previous outcome attenuates the ability to reach this energy intake threshold, then the animal may exhibit subsequent risk seeking behavior in order to compensate for this prior loss (Houston & McNamara, 1982). Therefore, like prospect theory, optimal foraging theory also seemingly predicts risk-seeking following losses. However, regardless of a zero-based reference point, uncertain-choice-based reference point, or certain-choice-based reference point, the results of Experiments 1 and 2 suggest that the rats made more probabilistic choices, and were thus more risk seeking, following gains (U-L) than following losses (U-Z; Figures 2.3 and 3.3). Thus, neither prospect theory nor optimal foraging theory seems to account for the present effects of previous outcomes on subsequent choice behavior.

In contrast to these predictions by prospect theory and optimal foraging theory, other theoretical frameworks of choice behavior predict greater risk-seeking following gains than following losses, such as the reinforcement learning model (Sutton & Barto, 1998) and the quasi-hedonic editing hypothesis (Thaler & Johnson, 1990; also see Hollenbeck, Ilgen, Phillips, & Hedlund, 1994; Slattery & Ganster, 2002; but see Sullivan & Kida, 1995). The reinforcement learning model is based on the classic linear operator learning model by Bush and Mosteller (1951), and thus accounts for learning the value of a choice. Assuming that an individual maintains an expectation of a choice's value, any deviation from this expectation causes a prediction error that is used to update reward expectancy (e.g., Barraclough, Conroy, & Lee, 2004; Glimcher, 2011). As higher valued outcomes are more likely to be chosen over lower valued ones, recent outcomes that increase or decrease the subjective value of a choice would thereby increase or decrease, respectively, the propensity to make that choice again. In the quasi-hedonic editing hypothesis, the differences in choice behavior following prior losses and prior gains are due to differential integrations of prior outcomes with prospective outcomes; risk seeking following gains reflects individuals' perceiving subsequent losses as simply decreases in current gains, while risk aversion following losses reflects aversion to additional losses (Thaler & Johnson, 1990, p. 656-657). Therefore, win-stay / lose-shift behavior is a direct prediction of both the reinforcement learning and quasi-hedonic editing hypothesis frameworks, as was observed here (Figures 2.3 and 3.3). However, each model does not fully account for the present results in certain respects. For instance, the reinforcement learning model proposes that uncertain gains and losses are regarded as such relative to the learned value of uncertain choice (uncertain-choice-based reference point). Therefore, this prediction stands in contrast to the present results which suggest that the expected value of the alternative certain choice serves as a reference point for uncertain gains and losses. Additionally, a corollary of the quasi-hedonic editing hypothesis is that individuals will exhibit risk seeking behavior following losses if subsequent choices permit the ability to "break even" (also see Demaree et al., 2012; McGlothlin, 1956). As the rats in all groups of the present experiments had the opportunity to break even given prior losses by making a subsequent uncertain choice (the 11-pellet U-L outcome), a break-even effect would have been evident had the rats made more uncertain choices following losses (e.g., U-Z outcomes) than following gains (e.g., U-L outcomes), which was not shown here (Figures 2.3 and 3.3). Therefore, the proposed effects of previous outcomes on subsequent choice behavior by the reinforcement learning and quasi-hedonic editing hypothesis frameworks can only partially account for the molecular results in the present experiments.

A more recent theoretical framework that is especially relevant to the present studies is the tri-reference point theory (Wang & Johnson, 2012). Rather than assuming that an individual uses one reference point to distinguish gains from losses, the tri-reference point theory assumes that individuals use three reference points that partition the outcomes into failures, losses, gains, and successes (also see Sullivan & Kida, 1995; Mishra & Fiddick, 2012, for discussion of multiple reference points). The reference points that separate failures from losses, losses from gains, and gains from successes are referred to as the minimum requirement, the status quo, and the goal reference points, respectively. While a goal reference point may be comparable to an aspiration-based reference point (see Mishra & Fiddick, 2012), the status quo has been previously suggested to serve as a possible reference point in prospect theory (Kahneman & Tversky, 1979), and the minimum requirement reference point is comparable to the energy intake threshold in optimal foraging theory (see Wang & Johnson, 2012). Additionally, Wang and Johnson (2012) described that outcomes on opposite sides of a given reference point should have greater effects on behavior relative to outcomes between two reference points. The expected value of the certain choice in the present experiment meets such a criterion in regards to uncertain gains and losses. All groups exhibited differential choice behavior following uncertain outcomes greater than the expected value of the certain choice (gains) compared to uncertain outcomes less than the expected value of the certain choice (losses). Interestingly, the significant differences in choice behavior following U-Z and U-S outcomes in Groups 1-11 and 2-11 in Experiment 1 do not adhere to such a criterion; such results may suggest the presence of a second reference point comparable to a zero-based reference point, such that U-Z outcomes are regarded as much greater losses than U-S outcomes. Therefore, while this framework does not seem to make any explicit predictions concerning the effects of failures, losses, gains, and successes on subsequent choice behavior, the tri-reference point theory may serve as a comprehensive approach to understanding reference points for different outcomes.

An integration of existing theoretical frameworks

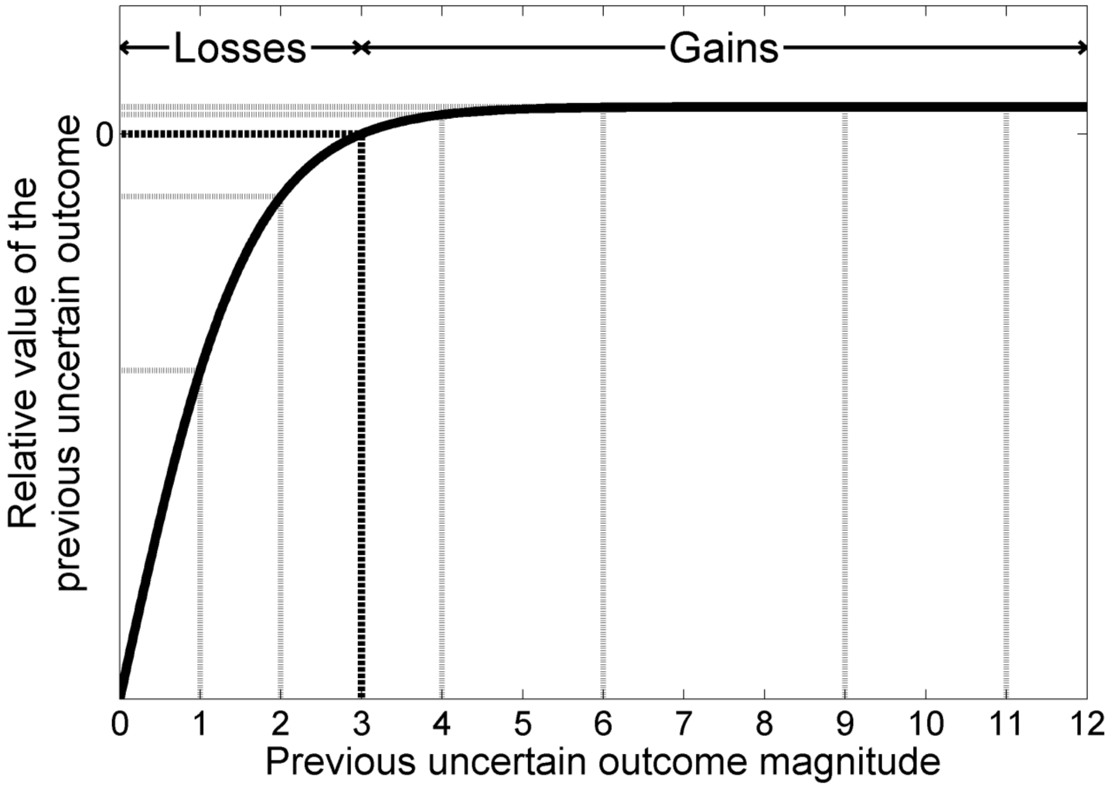
The theories of choice behavior described above posit distinct psychological mechanisms to account for probabilistic decision making. While each theory may not be able to fully account for the present data, there are individual elements of such frameworks that may be applicable to certain features of the present data. For example, in prospect theory, the subjective value of a gain is assumed to be a positively increasing, negatively accelerating function of the objective magnitude of the gain (Kahneman & Tversky, 1979); accordingly, the subjective value of greater outcome magnitudes is increasingly less than the objective value of the same outcome. While such concavity of the function has been used to explain overall risk aversion in the domain of gains (Kahneman & Tversky, 1979), this function may also be able to explain the effects of the previous outcome on subsequent choice behavior. The analyses of the data in Figures 2.3 and

3.3 suggest a differential sensitivity to prior outcomes that may be explained by a negatively accelerating function relating the magnitude of the previous outcome to its subjective value. For example, while Groups 1-11 and 2-11 in Experiment 1 exhibited significant differences in choice behavior across all uncertain outcomes, the other groups in Experiments 1 and 2 only exhibited significant differences in choice behavior between the U-Z outcome and the uncertain-food outcomes (see Figures 2.3 and 3.3). Furthermore, if the differential sensitivity to prior gains and losses can be represented by a concave function, then the corresponding reference point must fall along this function in order to distinguish the outcomes as gains or losses. Assuming that the reference point has the value of a positive outcome magnitude (X_{RP}), then the value of X_{RP} that maximizes the average difference between losses ($x < X_{RP}$) and gains ($x > X_{RP}$) would approximate the x-value of the point of maximum curvature of the concave function. Accordingly, outcomes with magnitudes less than X_{RP} would exhibit greater differences in subjective value than outcomes greater than X_{RP}, as was observed in the present study (see Figures 2.3 and 3.3). Therefore, setting the value of X_{RP} to the expected value of the certain choice would account for differential choice behavior following uncertain outcomes greater than and less than the expected value of the certain choice, assuming the concave value function described above.

Figure 4.1 shows how such a theoretical mechanism could account for the effects of previous uncertain outcomes on subsequent choice behavior. The concave value function is a cumulative logistic distribution function with a mean of 0 and a standard deviation of 0.8; the limits of this function as x approaches $+\infty$ and $-\infty$ are 1 and -1, respectively. The abscissa is the outcome of the previous trial, and the ordinate is the subjective value of the uncertain outcome relative to the expected value of the certain choice. As seen in the figure, the difference between the subjective values of previous uncertain losses (i.e., $x < X_{RP}$) is greater than the differences between the subjective values of previous uncertain gains, so that differential losses would be predicted to elicit greater differences in subsequent choice behavior than would differential gains (see Figures 2.3 and 3.3). Such a mechanism is consistent with Weber's law, which would predict that the same absolute difference in outcome magnitude would elicit smaller effects on choice behavior with increases in outcome magnitude (also see Hamm & Shettleworth, 1987, for an application of Weber's law to risky choice in pigeons). Accordingly, this mechanism may also be consistent with certain economic principles, such as diminishing marginal utility and the law of diminishing returns (for discussion and reviews, see Brue, 1993; Friedman & Savage, 1948; Kahneman & Tversky, 1979). Furthermore, this mechanism is consistent with the current and previously reported strong effects of reward omission within choice and non-choice paradigms (e.g., Amsel & Roussel, 1952; Marshall & Kirkpatrick, 2013; Staddon & Innis, 1966), as the greatest differences in subjective value relative to a certain-choice-based reference point would be produced by U-Z outcomes.

As this possible mechanism seemingly describes the present results, it may become necessary (given future research) to include such a mechanism within computational process-based models of choice behavior. For example, the reinforcement learning model computes the value of a choice as the sum of the previous estimate of value and the prediction error of the most recent outcome of the same choice (e.g., Glimcher, 2011); the prediction error describing the relative differences between gains and losses given the learned value of the choice involves a linear relationship between outcome magnitude and value. Accordingly, it is inconsistent with the possible mechanism described above. However, if it is assumed that an individual's reward expectancy does involve incorporating recent prediction errors with previous estimates of value of the same choice, as described by the reinforcement learning framework, then the explanatory power of this model may be strengthened upon the inclusion of a nonlinear prediction-error function describing the relationship between uncertain outcome magnitude and the learned value of an alternative certain choice. Such a valuation computation would be consistent with the observed overall sensitivity to probability of uncertain food delivery (and, therefore, expected value) as well as the local effects of previous uncertain outcomes. An incorporation of a certain-choice-based reference point in addition to a second reference point involving the learned value of a choice (comparable to an uncertain-choice-based reference point) may be accounted for within the multiple-reference-point framework of tri-reference point theory. Furthermore, a comparison of outcomes from one choice with the learned value of a second choice also seems relatively consistent with previously proposed decision rules, in which the values of multiple outcomes are compared to determine subsequent behavior (e.g., Luce, 1959; Herrnstein, 1961). Therefore, in addition to the possible mechanism described above, a differential sensitivity to uncertain gains and losses as described by prospect theory, a prediction error describing updates in value (reinforcement learning), and the use of multiple reference points (tri-reference point theory) may collectively account for the current molecular effects of previous outcome magnitude as well as the molar effects of probability (and thus, expected value) on choice behavior.

Figure 4.1 A possible mechanism to account for the asymmetric effects of the previous uncertain choice outcome on subsequent choice behavior. The abscissa is the magnitude of the previous uncertain outcome. The ordinate is the subjective value of the previous uncertain outcome relative to the expected value of the certain choice (3 pellets).



Chapter 5 - Conclusion

Probabilistic gains and losses have been shown to drive the decisions among choice outcomes that differ in the magnitudes and probabilities of their outcomes. Behavioral, neurobiological, and neuroeconomics accounts of such effects have shaped our understanding of probabilistic decision making (Campbell-Meiklejohn et al., 2011; Cardinal & Howes, 2005; Gehring & Willoughby, 2002; Hayden & Platt, 2009; Marshall & Kirkpatrick, 2013; McCoy & Platt, 2005; St. Onge et al., 2012; Stopper & Floresco, 2011; Stopper et al., 2012; Tom, Fox, Trepel, & Poldrack, 2007; Zhong et al., 2009; for theories and reviews, see Doya, 2008; Frank & Claus, 2006; Galtress, Marshall, & Kirkpatrick, 2012; Glimcher, 2011; Kahneman & Tversky, 1979; Levin et al., 1998; Levin et al., 2012; Rushworth & Behrens, 2008). In conjunction with these previous contributions to our understanding of probabilistic decision making, the present experiments have provided important insight into the mechanisms of choice behavior following uncertain gains and losses. To our knowledge, while differential sensitivities to gains and losses have been described (Kahneman & Tversky, 1979; Tversky & Kahneman, 1981, 1991), there has been relatively little discussion of reference-point use in animals, especially regarding the general notion that uncertain gains and losses are regarded as such relative to the expected value of the certain choice (but see Charnov, 1976; Cowie, 1977, for a related mechanism; also see Boles & Messick, 1995; Goyer et al., 2008; Mishra & Fiddick, 2012). This is not surprising, given that the common experimental designs and analyses of animal probabilistic-choice studies have not easily permitted such a conclusion to be made, either including too few choice outcomes, equating the expected values of multiple choice options, or failing to analyze the effects of previous outcomes on subsequent choice behavior. If such reference-point use for uncertain gains and losses does involve either a seemingly overlooked reference point such as the certain-choice-based reference point, or rather multiple reference points (see Wang & Johnson, 2012), then the possibility must be entertained that the extant models and frameworks of probabilistic choice behavior require modification. Thus, as probabilistic gains and losses may characterize either (or all of) human individuals' day-to-day activities (e.g., driving, diet selection, foraging), professional requirements (e.g., investment banking, the buying and selling of stocks), or problematic and/or pathological behaviors (e.g., drinking and driving, unprotected sex, gambling, drug abuse), it is essential to elucidate the psychological mechanisms that govern the effects of prior gains and losses on subsequent risky choice behavior. Only then may a complete understanding of risky decision making and a comprehensive neurocomputational account of choice behavior be possible.

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